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BULLETIN
OF THE
TORREY BOTANICAL CLUB

MARCH, 1922

Quadripartition by furrowing in *Sisyrinchium*

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(WITH PLATE 2)

Since the publication of the author's paper (5) on *Magnolia* there have appeared a few contributions to the subject of the quadripartition of pollen-mother-cells by furrowing. In 1918 Täckholm and Söderberg (24) presented an interesting discovery of the occurrence of quadripartition and bipartition respectively in two species of *Aristolochia*, a genus of Dicotyledons; *Aristolochia fimbriata* was found to have successive bipartition, just as Samuelson (19) had reported in this genus, but *Aristolochia Siphon* was found to have quadripartition of the pollen-mother-cells after the homoeotypic mitosis. It is stated that there is a slight thickening of the spindle fibers after the heterotypic division in the latter species, but no figures of quadripartition are shown in this paper. In *Vinca rosea* the authors conclude that quadripartition must occur because of the tetrahedral arrangement of the microspores within the mother wall. It will be remembered that Frye and Blodgett in 1905 (8) found successive bipartition in the sister genus *Apocynum*, and the microspores here are sometimes arranged tetrahedrally. The authors (24) state that after the homoeotypic division in *Aristolochia Siphon* walls are laid down as fine plates on the equator of the spindle, and that in *Albizzia lophantha*, a Dicotyledon, and *Dioscorea quinquefolia*, a Monocotyledon, quadripartition

[The BULLETIN for February (49: 31-50) was issued April 4, 1922.]

is accomplished by equatorial plates on the spindles. Quadripartition by cell-plates has never been satisfactorially described and figured in any of the higher plants in connection with a study employing modern methods of microtechnique; it is therefore much to be desired that the authors present these instances in detail as soon as possible.

Florin (7) in 1918 found that quadripartition occurs in the spore-formation of one of the acrogynous Jungermanniales but does not give the details of the process as to whether it is by furrowing or cell-plates. In 1919, Miss Digby (3) published an extensive chromosomal study of *Osmunda* in which she refers to the formation of cell-plates after the first reduction division. These apparently persist through the second mitosis without forming completed partitions, and then other cell-plates are formed at right angles to these. The figures of these stages are drawn from material of *O. palustris* var. *aurea* although the description seems to apply to all four of the types studied, including *O. regalis*. Smith (20) in 1900 described and figured these stages of the latter species. He concluded that the cell-plate of the first division was ephemeral and that the division was finally accomplished by the simultaneous formation of six cell-plates on the six spindles respectively, thus accomplishing quadripartition by cell-plates. During 1920 Yamaha (27) published a study of cell-plate formation in the archesporial and spore-mother-cells of *Psilotum triquetrum*. He found that the nearly complete cell-plate which is formed after the first meiotic division breaks up into a granular mass, which persists until the close of the second nuclear division. At this time it becomes transformed into connecting fibers upon which a cell-plate is laid down between the non-sister nuclei, while other cell-plates are being formed on the connecting fibers between the sister nuclei of the second division. In this way a quadripartition of the cell is accomplished by cell-plates. Yamaha concludes that the cell-plate has a duplex nature from the first, and that it does not split after formation as Timberlake believed. It is to be noted that in quadripartition by furrowing the partition is duplex from the first. Yamaha suggests that the invagination of the plasma-membrane may play some part in the later stages in these cells of *Psilotum*. It therefore seems to me that on account of this duplex nature of the partition and in the light of the recent work on quadripartition by furrowing that further work on cell-division of *Psilotum* would be warranted.

Guérin (10) has made a study of the development of the anthers and pollen of the labiates, but passes over the matter of division of the mother-cell into the four microspores as exhibiting nothing of particular interest. Valteau (26) in connection with his study of sterility in the strawberry has published a careful account of pollen-formation. He describes in detail the formation of the material about the protoplast which in other forms has been considered as the thickening of the cell-wall. However, in *Fragaria*, it seems to be a secretion from the protoplast rather than the thickening of the wall. With regard to the formation of the partitions the author does not commit himself. He states:

The daughter nuclei are soon formed, and walls are laid down between them, dividing the cytoplasm evenly. The cells gradually split apart, separating the four microspores and allowing the entrance between them of the viscous material.

It might be concluded from this description that cell-plates accomplish the partitioning and that the invagination of the peripheral material is simply incidental to the rounding up process. No figures of these stages are shown. Quite recently R. R. Gates (9) has published a preliminary account of reduction divisions in the pollen-mother-cells of *Lactuca sativa*. In this paper there is described a quadripartition by furrowing rather than by cell-plates, just as the writer (4) had previously reported for *Helianthus* and *Ambrosia*, as well as in other groups of Dicotyledons. No drawings are given by Gates, but a paragraph is devoted to a description of the process. He mentions that furrows may be formed either in the presence or the absence of spindle fibers but does not describe the latter instance any farther. It is stated that an ephemeral cell-plate occasionally is found after the heterotypic division, but it never functions and no cell-plate is present after the homoeotypic mitosis.

The most careful recent study of this question is that of Mrs. Wanda K. Farr (6), in which she gives figures and descriptions of quadripartition in the pollen-mother-cells of *Cobaea scandens*. These support the writer's contention (4) that cell-division by furrowing is common in the pollen-mother-cells of Dicotyledons. It is interesting to note that the first description of cell-division in any plant is probably that by Brongniart in 1827 on the pollen-mother-cells of *Cobaea scandens* (2), in which it is indicated that the process is furrowing, though, of

course, he had no realization of the internal mechanism of the cell. This work was followed by that of Mirbel (17) who presented his paper in 1832, though it was not published until later. He described and figured quadripartition by furrowing in the pollen-mother-cells of *Cucurbita Pepo*. A little later Von Mohl (18) published figures and descriptions of the same process in other plants. It now seems that the interpretation given by these first observers was more nearly correct than that which has been given by most students of cell-division in higher plants in more recent years.

Up to the present no detailed study has been made of quadripartition in Monocotyledons, and it was with the idea of comparing the situation in this group with that found in Dicotyledons that the present study was undertaken. Several cases of quadripartition in Monocotyledons are known. In 1915, L. Guignard published two papers (12, 13) on the occurrence of quadripartition in Monocotyledons. In the first paper he includes a comprehensive review of the literature on that subject, as well as on bipartition in the reduction-divisions of Dicotyledons. Quadripartition in Monocotyledons and bipartition in Dicotyledons at the time of reduction-divisions are unquestionably the exception in the method of pollen formation in these two groups respectively. So rare is their occurrence in fact that Van Tieghem (25) used them as characters of prime importance in distinguishing the two classes of Angiosperms, thereby including the Nympheaceae with the Monocotyledons. Guignard had previously (11) reported quadripartition in six genera of the Orchidaceae, and in the first (12) of his recent publications adds four genera (six species) of Liliaceae and six genera (sixteen species) of the Iridaceae. To this list the second paper (13) contributes three more genera (three species) to the number of the Iridaceae having this method. To the Liliaceae may be added Strasburger's (21, p. 151) findings in *Asphodelus*, and it will be remembered that Hofmeister found it in *Naias* (14, p. 636). In 1917, Täckholm and Söderberg published a paper (23) in which they discuss tetrad formation in Monocotyledons. In addition to its occurrence in the above-mentioned groups they refer to quadripartition being reported by Hofmeister in *Tradescantia*, by Rosenberg in *Anthericum* and by Von Mohl and others in the Juncaceae. So that they find it reported in six families of the Monocotyledons, namely: Liliaceae, Juncaceae, Iridaceae,

Commelinaceae, Orchidaceae, and Cyperaceae. The last-named is included because of the work of Juel on *Carex*, of which it may be questioned whether the term quadripartition is applicable. In 1918 the same authors (24) published again, adding another species of Monocotyledons to this list, namely, *Dioscorea quinquefolia*. This brings the total number of genera up to nineteen or twenty. In *Canna* they report a tetrahedral arrangement of the microspores but do not take this as evidence of quadripartition.

Guignard (12) states that in four species of *Iris* there is occasionally a suggestion of a partition after the heterotypic nuclear division but this is always ephemeral. After the homoeotypic mitosis in *Sisyrinchium*, *Antholyza*, *Freesia*, *Ixia*, and *Monbretia*, when the fibers of the central spindle are formed between the four nuclei, it is stated that rather frequently there is noticeable a faint thickening on the internal face of the mother wall at the places which are to become the points of insertion of the partitions. Further than this no details of quadripartition are given, nor are drawings or photomicrographs shown to give evidence as to whether the process is accomplished by cell-plates or by constriction furrows. It is not unlikely that the ephemeral equatorial differentiations which Guignard found in these Iridaceae, and which Täckholm and Söderberg reported for *Aristolochia Sipho* are orange zones, such as the writer (5) has shown to occur in *Magnolia*. Täckholm and Söderberg (24) do not describe the process of quadripartition in *Dioscorea* except to state that it is accomplished by equatorial plates being formed on the spindles.

It thus appears desirable that a study be made of the details of the process of quadripartition in a Monocotyledon. The writer has discussed at some length the literature on this subject in his first paper in 1916 (4). At that time he presented a description and drawings of quadripartition in *Nicotiana* and other Dicotyledons which led to the conclusion that no cell-plates are formed, but that division is accomplished by furrows very much as in animal cells. Mrs. Wanda K. Farr (6) has more recently shown that the same type of cytokinesis occurs in *Cobaea scandens* as was found in *Nicotiana*. In 1918, the writer (5) supplemented the work of Guignard on *Magnolia*, in which the latter showed incipient furrows during interkinesis, but did not present the stages following the origin of the tetranuclear

condition. It was found that after the disappearance of the ephemeral orange zone a furrow developed on the margin of the equator of the heterotypic spindle. However, the development of this furrow is arrested when it is only about one-fourth completed and the homoeotypic nuclear division ensues. The division of the cell is finally accomplished by the completion of this furrow and the formation of two other furrows at approximately right angles to it. Although *Nymphaea* has not as yet been thoroughly investigated the work of Lubimenko and Maige (16) indicates that it is similar in this respect to *Magnolia*.

The following study was made upon material of *Sisyrrinchium Bushii* Bicknell, collected near College Station, Texas, and identified by Dr. A. S. Hitchcock. This species proved especially fine for study, both because of the excellent fixation and because of the distribution of the mitotic figures in the anthers. In *Nicotiana* the mother-cells of a given anther are all in very nearly the same stage of division, and hence to secure an unbroken series of stages it is necessary to take material from several different anthers. In *Magnolia* the mother-cells within the anther were at different stages but there was no special arrangement of them. In either of these cases the objection might be raised that a cell-plate was overlooked due to the study of an incomplete series of stages. It was therefore highly desirable that a form be found in which the stages were arranged in order within the anther from one end to the other, so that by studying a number of anthers it could be determined with certainty that no steps have been omitted. Such a situation is that which *Sisyrrinchium Bushii* presents. The mother-cells at one end of the anther may be in metaphase of the heterotypic division and those at the other end in metaphase of the homoeotypic. This is the condition shown in FIG. 1. In FIG. 2, the cells at the inner end are in metaphase of the homoeotypic division and those at the outer end are in the tetranuclear stage. It is evident that the study of a number of such anthers is sure to reveal every stage, however transitory. It will be remembered that a similar condition exists in the testes of *Batrachoseps*, and among plants it was found by Strasburger (22) in the anthers of *Fritillaria* and by D'Angremond (1) in the banana.

The pollen-mother-cells of *Sisyrrinchium* are smaller than those characteristic of many Monocotyledons. Miss Klieneberger (15) has recently published a study of the size of nuclei

of Monocotyledons, in which she finds that contrary to the general opinion the nuclei of most Monocotyledons are small. It is only in the Iridaceae and parts of the Liliaceae, Amaryllidaceae and Convallariaceae that large nuclei are found. However, her study is not concerned with pollen-mother-cells especially. It would be interesting to find how great the differences in size of pollen-mother-cells may be among Monocotyledons, and their relation to the size of the nuclei. The tetranucleate pollen-mother-cells of *Sisyrinchium* just before division are 36–40 microns in diameter, which is just about the size of those of *Nicotiana*.

The mother-cell wall is likewise thickened to about the same extent as is that of *Nicotiana*, that is, on the average about one-tenth of the diameter of the cell. The process of thickening of the cell-wall begins about the time of synapsis, but the greatest development is during interkinesis. The cells are more compact within the anther than they are in either *Nicotiana* or *Magnolia*, but nevertheless are quite loosely disposed during diakinesis and later stages of reduction. They are somewhat closer together toward the end of the process than in the earlier stages doubtless due to the enlargement of the cells and the thickening of the walls. There seems to be no evidence that the gelatinous substance enveloping the protoplast during the later stages of reduction-divisions is a secretion from the protoplast, as Valteau (26) suggests, rather than a product of the cell-wall. The middle lamellae remain quite distinct throughout these stages and careful observation of the material both of *Sisyrinchium* and of the other forms previously studied leads the writer to the conclusion that it is the secondary lamellae of these pollen-mother-cells which during reduction-divisions take on the colloidal property of imbibition and swell to many times their original thickness.

The heterotypic division results in two discoid nuclei being organized at opposite ends of a rather long central spindle. No indication of a cell-plate or other equatorial differentiation is to be discerned at any time during interkinesis. Nor is there any indication of furrowing. The nuclei gradually become more nearly spherical (FIG. 1) and finally, before the second nuclear division begins, they are almost perfect spheres. They apparently do not come into contact with the plasma membrane. The fibers of the central spindle disappear almost entirely during in-

terkinesis, and the integrity of the spindle as such becomes entirely lost. The fact that all stages of interkinesis may be found within the extent of a single anther (FIG. 1) makes it possible to arrive at an index of the relative time required for that stage. Judging from the extent of the various stages within the anther it would seem that the time involved in interkinesis is about equal to that involved in either the first or the second reduction-division.

In the metaphase of the homoeotypic nuclear division the spindles are in some cases parallel and in some at right angles to each other, and in still others at positions intermediate between these two extremes. When the nuclei are reconstituted they may occasionally be found in a single plane as is shown in the outer end of the anther in FIG. 2. But more frequently the nuclei are tetrahedrally arranged (FIG. 3). Quite a number of cells show intermediate orientations. It is interesting to note that the type of division of the cell is the same, regardless of the orientation of the nuclei, just as was previously reported for *Magnolia* (5).

The nuclei become reorganized in much the same manner as after the heterotypic division. They, however, do not become as large as in the previous division and they move apart so that they become closely appressed to the plasma membrane. Almost as soon as the nuclear membranes appear spindles are organized connecting the nuclei which are not already connected by the two homoeotypic spindles. There are thus six spindles in all within the cell, but the integrity of some of these seems almost lost especially in cases where the four nuclei are in one plane.

The time elapsing between the conclusion of nuclear division and the beginning of cytokinesis is evidently relatively long. This is indicated by the fact that all of the cells of a single anther may be in these stages, those at one end just coming out of karyokinesis and those at the other end not yet showing signs of the formation of partitions. It thus appears that this period is at least as long as that involved in either the heterotypic or homoeotypic mitosis; which is quite in harmony with the writer's previous suggestion (5) that cell-plate formation and furrowing do not occur at corresponding periods in the cell-cycle, but that cell-plate formation follows very soon after nuclear division, if indeed the two processes may not frequently overlap. Furrow-

ing on the other hand takes place only after a considerable time has elapsed following the re-formation of the nuclei. If cell-plates appeared in this division we would most certainly expect to find them in such an anther as that shown in FIG. 2, but none such are present.

The process of cytokinesis in the quadripartition of the pollen-mother-cells of *Sisyrrinchium* is by furrowing and is practically identical with that found in *Nicotiana*. It does not seem necessary to repeat the details of the description of the process here, inasmuch as there is no difference from that which has been published before (4). In cells where the nuclei are tetrahedrally arranged the plasma membrane invaginates most rapidly at the points equidistant from the three nuclei and therefore a central triangular area is formed (FIG. 3). In cells in which the nuclei are in one plane no such central triangular area appears, but the spindles have the same relation to each other, as was shown in those cells of *Magnolia* (5) in which the arrangement was of this type.

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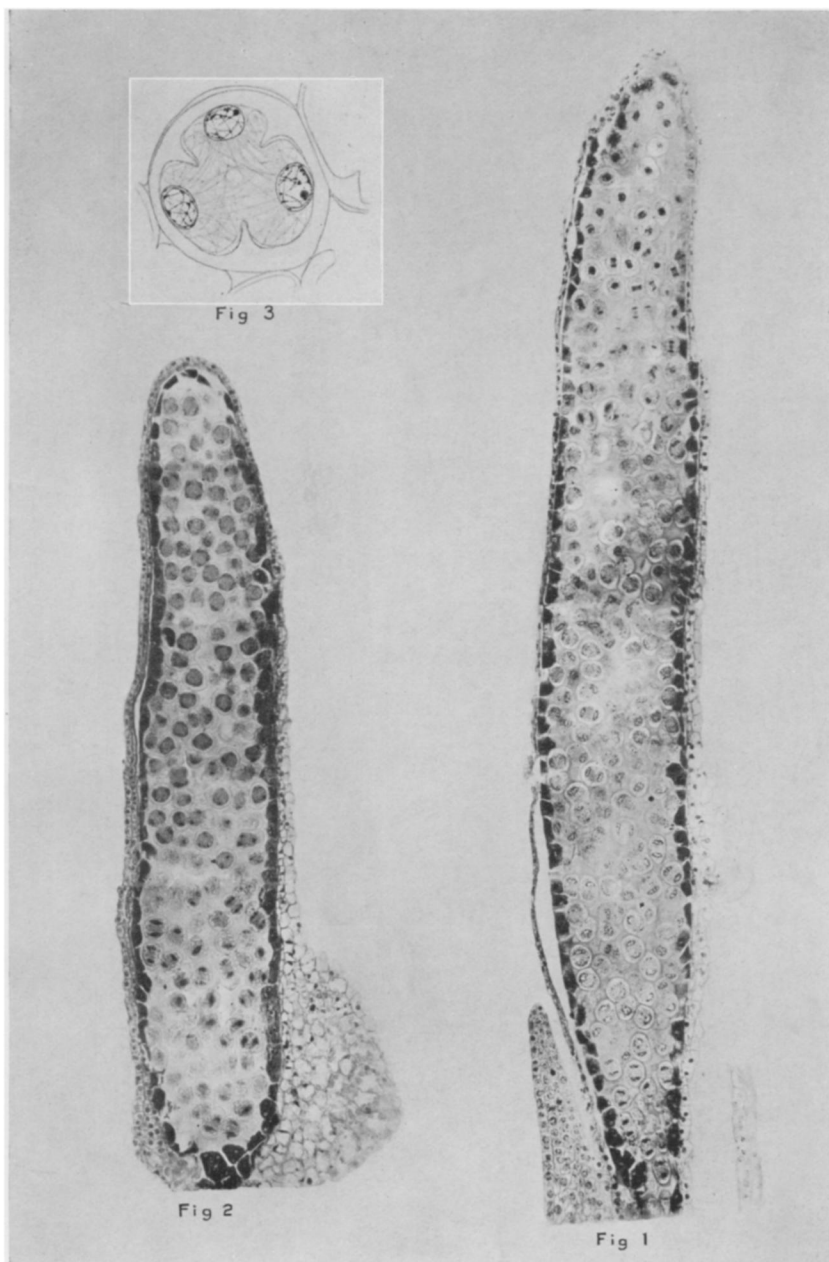
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Description of plate 2

FIG. 1. Photomicrograph of a longitudinal section of an anther of *Sisyrrinchium Bushii*. The cells in the outer end are in the metaphase of the heterotypic and those at the inner end are in metaphase of the homoeotypic division.

FIG. 2. Photomicrograph of an anther at a slightly later stage of development. The cells at the inner end are in metaphase of the homoeotypic mitosis and those at the outer end are in the tetranucleate stage just prior to furrow formation.

FIG. 3. A drawing of a cell in cytokinesis. The furrows are partly formed and the central triangular area is appearing.



FARR: QUADRIPARTITION IN SISYRINCHIUM